

Variance Components for Yield and Specific Gravity in a Diploid Potato Population after Two Cycles of Recurrent Selection

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ABSTRACT

The potato (*Solanum tuberosum* L.) processing industry needs cultivars with high tuber specific gravity and acceptable color of processed product. All of the cultivars with high specific gravity currently grown in the U.S. are very closely related, which increases their genetic vulnerability and results in inbreeding as efforts are made to improve these traits. The use of diploid *Solanum* sp. in breeding may resolve these problems. The purposes of this study were (1) to estimate narrow-sense heritability for yield and specific gravity in random-mating diploid hybrid potato populations of *S. phureja* - *S. stenotomum* (PHU-STN) following two cycles of recurrent selection, (2) to examine phenotypic variances for yield and specific gravity following two cycles of recurrent selection within PHU-STN, (3) to compare the yield and specific gravity of individual PHU-STN clones with Atlantic, and (4) to screen these PHU-STN clones for the presence of 2n pollen. Four clones from each of 72 maternal half-sib families were evaluated for yield and specific gravity in replicated field tests in 1990 and 1991. A second selection cycle, using a randomly mated population obtained from the highest specific gravity clone in each maternal half-sib family, was similarly evaluated for yield and specific gravity in replicated field tests in 1995 and 1996. Narrow-sense heritability for specific gravity was estimated as 0.37 ± 0.25 and 0.43 ± 0.27 , in the first and second selection cycles, respectively, with a 27% decrease in phenotypic variance. Narrow-sense

heritability for yield was estimated as 0.60 ± 0.26 and 0.06 ± 0.24 , in the first and second selection cycles, respectively, with a 73% decrease in phenotypic variance. There were significant correlations between yield and specific gravity in 1990 ($r=0.32$) and 1996 ($r=0.37$), but not 1991 ($r=0.08$) and 1995 ($r=0.05$). These results indicate that additional breeding efforts in this PHU-STN population could result in improvements in specific gravity. However, the amount of variation for yield in this population is decreasing and may indicate that the yield potential of this population is rapidly approaching its limit. In the second selection cycle, many of the 288 clones were significantly higher in specific gravity than the high-specific-gravity cultivar Atlantic, but none were higher yielding. Fifty-eight clones from the second selection cycle produced at least 5% 2n pollen. When used in tetraploid x diploid hybridizations, this diploid population could furnish new genetic material to the tetraploid potato germplasm base for simultaneously increasing specific gravity and yield.

INTRODUCTION

Potato (*Solanum tuberosum* L.) cultivars that combine high tuber yield with high specific gravity are needed by the potato-growing community and the commercial potato-processing industry. High tuber dry matter content, as measured by tuber specific gravity, results in more processed product per unit; more rigid, crisp, and mealy french fries (Johnston *et al.* 1970; Mohr 1972; Sayre *et al.* 1975); less oily potato chips (Kunkel *et al.* 1951); and more starch (Reeve *et al.* 1970). A recent study by Douches *et al.* (1996) has suggested

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Article abbreviations:

PHU-STN, *Solanum phureja* - *Solanum stenotomum*; SG, specific gravity.

that little progress has been made in the 20th century in breeding potatoes for increased yield. However, more recently developed potato cultivars have shown improvement for traits that are important to the processing industry, such as high specific gravity and chip color.

Commercial potato cultivars are tetraploid ($2n=4x=48$). The relatively narrow-genetic base of commercial tetraploid potatoes in the United States has been well documented (Mendoza and Haynes 1974) and is cause for concern. A negative relationship between yield and specific gravity was reported in advanced tetraploid potato selections (Haynes *et al.* 1989b) and in tetraploid tuberling populations selected on the basis of horticultural characteristics (Haynes and Wilson 1991) from the USDA potato-breeding program in Beltsville, MD. Plaisted and Hoopes (1989) have documented the use of new sources of potato germplasm in cultivar development in recent years. These new sources of germplasm are necessary to expand the breeding effort and avoid inbreeding in subsequent potato cultivar releases.

Two diploid potato species, *Solanum phureja* and *S. stenotomum*, are among the possible progenitors of tetraploid *S. tuberosum* (Dodds 1962). Haynes (1972) began a breeding program in 1966 utilizing approximately 30 plant introductions each of *S. phureja* and *S. stenotomum* from the IR-1 collection at Sturgeon Bay, WI. The addition of a few other introductions from these two species early in the enhancement effort brought the final number of introductions to 72 (Haynes 1980). These introductions underwent six two-year cycles of recurrent selection for adaptation to the long-day growing conditions of North Carolina.

Ruttencutter *et al.* (1979) obtained estimates of narrow-sense heritability for specific gravity in this PHU-STN population when grown in the mountains of North Carolina that ranged from 0.28 to 0.74. The estimates least biased by genotype x environment interactions averaged 0.43. Haynes *et al.* (1989a) estimated narrow-sense heritability for specific gravity in this PHU-STN population under the high-temperature growing conditions in eastern North Carolina as 0.28. This estimate was unbiased by genotype x environment interactions. In a later study, Haynes *et al.* (1995) estimated broad-sense heritability for specific gravity in this PHU-STN population under the more moderate growing conditions in northern Maine as 0.66 and found no relationship between the stability of a clone and its specific gravity. Haynes and Haynes (1990) also reported that they were able to select for tuber characteristics and maintain high specific gravity in this PHU-STN population.

Through 4x-2x hybridizations between tetraploid *S. tuberosum* and various diploid potato species that produce numerically unreduced pollen (Peloquin *et al.* 1989), valuable traits in the diploid species can be genetically transferred into tetraploid potatoes while simultaneously expanding the tetraploid germplasm breeding base. Various researchers have discussed the genetic basis for either a heterotic response (Peloquin *et al.* 1989; Tai 1994) or inbreeding depression (Haynes 1992; Haynes 1993; Tai 1994) from such crosses. Wannamaker and Collins (1992) reported that 4x-2x crosses involving this diploid germplasm base with high specific gravity resulted in progeny with high specific gravity. Population improvement at the diploid level needs to continue to effectively utilize such germplasm (Ortiz *et al.* 1988). Depending on the traits being studied, the ability of the diploid parent to pass on a trait to its offspring through 4x-2x hybridizations may be quite high (Iwanaga *et al.* 1989; Ortiz *et al.* 1988; Herriott *et al.* 1990; Wannamaker and Collins 1992) or quite low (DeJong and Tai 1991).

This study was conducted as part of the continuing effort to improve the diploid PHU-STN population. The objectives of this study were (1) to estimate narrow-sense heritability for yield and specific gravity in random-mating diploid hybrid potato populations of PHU-STN following two cycles of recurrent selection for high specific gravity, (2) to examine phenotypic variances for yield and specific gravity following these two cycles of recurrent selection within PHU-STN, (3) to compare the yield and specific gravity of individual clones from the second selection cycle of this PHU-STN population with Atlantic, a high-yielding, high-specific-gravity cultivar for chipping (Webb *et al.* 1978), and (4) to screen the PHU-STN clones from the second selection cycle for the presence of 2n pollen.

MATERIALS AND METHODS

An overview of the breeding scheme used in this study is presented in Figure 1.

During the first week of October 1988, true seed from 72 hybrid diploid random-mating families of *S. phureja* - *S. stenotomum* were treated with 1500 mg kg⁻¹ gibberellic acid (GA₃) for 24 h, rinsed with tap water, allowed to air dry, and sown in flats of Jiffy Mix (Jiffy Products of America, Inc., West Chicago, IL) in the greenhouses at Beltsville, MD. Approximately 150 seedlings from each family were transplanted into Jiffy Mix in 8.9-cm clay pots from 20-21 October. Seedlings were harvested 9-10 February 1989. The largest

Figure 1. Diagram of the breeding scheme utilized in this study.

Year		Breeding Scheme
First Selection Cycle	Second Selection Cycle	
1988	1992	Produce seedling generation in greenhouse
1989	1993	Grow seedling generation in field in Presque Isle, Maine (72 families x 100 seedlings/family) Select 4 'best' clones per family
1990	1995	Evaluate 288 clones in randomized complete block design Collect open-pollinated fruit from all 288 clones Measure yield and specific gravity
1991	1996	Evaluate 288 clones in randomized complete block design Measure yield and specific gravity Choose highest specific gravity clone from each family to plant open-pollinated seed from that clone to start cycle all over again

tuber harvested from each pot was saved for planting in the field. Tubers from the same family were bulked, stored in muslin bags at 4 C and 95% relative humidity, and subsequently shipped to Presque Isle, Maine, in the spring for field planting.

For all years of the study, all clones were grown in the field on the Chapman Farm, Presque Isle, Maine, in a Caribou silt loam soil (fine-loamy, mixed, frigid Typic Haplothod) following a plowed down timothy-clover sod with a soil pH ranging from 5.0 to 5.4. The test location was fertilized with 1200 kg ha⁻¹ of 14-14-14 N-P-K banded in row at planting. Cultural practices were similar to those used on commercial farms in the area. No irrigation was available.

On 25 May 1989, 100 tubers from each family were planted in a randomized complete block design, with four replications, each having 25 single hills per family. Plants were spaced 30 cm within the row on rows 91 cm apart. At harvest, 22 to 25 September, one hill within each 25-hill plot per family was selected on the basis of horticultural characteristics, such as smoothness, size, non-sprouting, relative earliness, and freedom from defects, resulting in four clones per family. Tubers were stored in paper bags at 4 C and 95% relative humidity.

On 29 May 1990 and 20 May 1991, the four clones from each of the 72 families constituting the first selection cycle

were planted in a randomized complete block design, with two replications of five hills per clone. On 18 September 1990, 10-20 fruit were harvested from each plot and seed were extracted one to two months later. Tubers were harvested on 19 September 1990 and 12 September 1991, respectively, yield was measured and specific gravity was determined during December 1990 and January 1991, and October 1991, respectively, using the weight-in-air/weight-in-water method (Murphy and Goven 1959). Tubers were stored in paper bags at 4 C and 95% relative humidity.

Within each maternal half-sib family, the clone with the highest average specific gravity in 1990 and 1991 was chosen to be a parent for the next generation. One hundred fifty open-pollinated seed (potentially 288 male parents in the open-pollinated seed) from the 1990 seed nursery were treated with 1500 mg kg⁻¹ GA₃ as before, and sown in flats of Jiffy Mix in mid- August 1992 in the greenhouses at Beltsville and subsequently transplanted into 8.9-cm clay pots. The largest tuber per plot was harvested during the first two weeks of December. Tubers were bulked by family, put into muslin bags, and placed in 4 C and 95% relative humidity storage. Tubers were shipped to Presque Isle, Maine, in April 1993.

On 26 May 1993, these seedling tubers were planted contiguously in rows 91 cm apart at 30 cm within the row. At harvest, 17 September, four hills within each family were again selected on the basis of horticultural characteristics, such as smoothness, size, non-sprouting, relative earliness, and freedom from defects. Tubers were again stored in paper bags at 4 C and 95% relative humidity.

On 10 June 1994, the four clones from each of the 72 families constituting the second selection cycle were planted in a randomized complete block design, with two replications of six hills per clone. Most of the second replication was destroyed by Colorado potato beetle (*Leptinotarsa decemlineata* Say) feeding in August. Consequently, seed tubers were harvested from the first replication for planting in 1995, and no data were collected.

On 2 and 5 June 1995 and 10 June 1996, the clones from the second selection cycle were planted in a randomized complete block design, with two replications of six hills per clone. Seven and eight plots of the tetraploid high-yielding, high-specific-gravity chipping cultivar Atlantic (Webb *et al.* 1978) were planted in each replication in 1995 and 1996, respectively. Tubers were harvested on 13 and 15 September 1995 and 18 and 20 September 1996, yield was measured, and specific gravity was determined during November and

December 1995 and October and November 1996, respectively.

A single tuber from each of the 288 clones in the second selection cycle was planted in the greenhouse in Beltsville, MD, in January 1995. Pollen was subsequently collected, stained with propiono-carmin (Swaminathan *et al.* 1954), and the presence of 2n pollen was visually estimated (Quinn *et al.* 1974).

Yield and specific gravity were analyzed by selection cycle using the mixed procedure in SAS (Littell *et al.* 1998). Year, replication, family and clones(family) were all treated as random variables for the analyses. Residuals from the analyses were plotted against their predicted values and examined for homogeneity. These plots suggested that the residuals were homogeneous. Estimates of the family and clones(family) variance components from these analyses were equated to their additive and dominance variance components: the variance among families, $\sigma_F^2 = (\sigma_A^2) / 4$, where σ_A^2 is the additive genetic variance; the variance within families, $\sigma_{C(F)}^2 = (3 \sigma_A^2) / 4 + \sigma_D^2$, where σ_D^2 is the dominance variance. Narrow-sense heritability (h^2) was estimated as σ_A^2 / σ_P^2 , where σ_P^2 is the phenotypic variance (Nyquist 1991). The standard error of h^2 can be estimated as 4 (s.e.) σ_F^2 / σ_P^2 .

The correlations between yield and specific gravity in each of the four years of this study were calculated (SAS 1987). Least significant differences among clones were calculated for the second selection cycle to compare the mean yield and specific gravity of each of the individual PHU-STN clones to Atlantic by year.

RESULTS AND DISCUSSION

The two growing seasons in which each selection cycle were evaluated were very different from each other. Temperatures immediately following planting in 1990 were lower than normal, then turned higher than normal during the period of tuber bulking. Rainfall was fairly uniform. In 1991, crop growth was limited by hot, dry conditions from June through mid-August. Then, 21.7 cm of rain fell in late August. In 1995, temperatures were warmer than normal for most of the growing season and rainfall was only about half of normal. In contrast, the 1996 growing season was nearly ideal for potato production with warm days, cool nights and fairly uniform rainfall over the growing season. Overall, the 1990 and 1996 growing seasons were considered fairly good for potato production. The 1991 and 1995 growing seasons were

TABLE 1.—*Estimates of the variance components from the analyses of variance on yield and specific gravity^a for 288 diploid hybrid PHU-STN potato clones from the first and second selection cycles grown in Presque Isle, Maine, in 1990 and 1991 (first selection cycle) and 1995 and 1996 (second selection cycle).*

Component	First Selection Cycle		Second Selection Cycle	
	Yield	Specific Gravity	Yield	Specific Gravity
Year	2192	0.00	6005	2.74
Rep(year)	0	6.81	698	12.87
Family	5742*	10.18	142	8.58
Year x family	0	0.42	772	6.71*
Clones(family)	23279**	74.75**	5421**	47.42**
Year x clones (family)	11955**	21.94**	2596**	23.36**
Error	13025	51.08	11733	34.85
σ_A^2	22968	40.71	570	34.31
σ_D^2	6053	44.21	4994	21.68
σ_P^2	38255	108.88	10181	79.74
Mean of PHU-STN	389	85	413	93
Mean of Atlantic	-	-	868	86

*, **Significant at the 5% and 1% levels, respectively.

^aVariable analyzed was (1000 x specific gravity) - 1000.

considered poor for potato production. However, there was no significant year effect for either yield or specific gravity in either selection cycle (Table 1).

In the first selection cycle there were significant yield differences among families, but not in the second selection cycle, and there were no differences among families for specific gravity in either selection cycle (Table 1). The lack of significant differences among families for specific gravity may be the result of prior selection for specific gravity within this population while under development in North Carolina (Haynes *et al.* 1995). The lack of significant differences among families for yield in the second selection cycle may indicate that adaptation for the growing conditions in northern Maine was achieved after only one cycle of selection. Initial selection criteria among the 100 segregating seedlings per family prior to the establishment of the two selection cycles was limited to horticultural characteristics such as smoothness, size, non-sprouting, relative earliness, and freedom from defects. Yield *per se* was only one of several variables upon which initial selection was based, and high-yielding seedlings in which tubers were already sprouted at harvest,

extremely late (as measured by the difficulty in removing them from the plant), or subject to some external defect were not saved for this study.

There were significant differences among the clones within a family for both yield and specific gravity, indicating that some type of mass selection, rather than family selection, would be appropriate for selecting high-yielding clones with high specific gravity for the next breeding and selection cycle.

The year \times clones(family) interactions were significant for both yield and specific gravity in both selection cycles, indicating that the clones were responding differently to the favorable and less favorable growing conditions represented by the two years in each selection cycle.

From the estimates of the variance components (Table 1) narrow-sense heritability for yield in the first and second selection cycles was estimated as 0.60 ± 0.26 and 0.06 ± 0.24 , respectively. There is a dramatic decrease in the estimate of heritability for yield between the two selection cycles. The estimate of phenotypic variance for yield in the second selection cycle was 10,181, which is only 27% of the estimate of phenotypic variance (38,255) in the first selection cycle. Such an alarming drop in phenotypic variation in this population from the first to the second selection cycle may limit breeding progress for yield in the near future if similar reductions in magnitude occur in future selection cycles. This problem needs to be investigated in additional studies, along with different breeding strategies to overcome this obstacle.

From the estimates of the variance components (Table 1) narrow-sense heritability for specific gravity in the first and second selection cycles was estimated as 0.37 ± 0.25 and 0.43 ± 0.27 , respectively. The estimates of heritability for specific gravity in the two selection cycles are similar and in general agreement with the estimates of heritability obtained by others (Ruttencutter *et al.* 1979; Haynes *et al.* 1989a). These estimates indicate that additional progress in improving specific gravity in this population should be possible.

The rather high standard errors associated with all of these estimates of narrow-sense heritability may be a result of there being a favorable and unfavorable growing environment for potato production in both selection cycles. The genotype \times environment interaction, in this study represented by the combined year \times family and year \times clones (family) variations, made a significant contribution to the phenotypic variance for both traits.

The correlations between yield and specific gravity were significant in 1990 ($r=0.32$) and 1996 ($r=0.37$), but were not significant in 1991 ($r=0.08$) and 1995 ($r=0.05$). The two years

in which these correlations were significant represented the favorable growing season in each cycle. When growing conditions are not favorable for production of a crop, less variation in the traits measured would normally be expected, and could lead to no correlation among the traits. Favorable growing conditions allow for greater variation in the traits as superior genotypes are able to respond more than inferior genotypes. However, whether in favorable or unfavorable growing conditions, these results are opposite to the situation that has been observed in advanced selections from tetraploid breeding programs, where a negative correlation between yield and specific gravity has been reported (Haynes *et al.* 1989b; Haynes and Wilson 1991).

In the second selection cycle the average yield of Atlantic was 712 and 1024 g/hill in 1995 and 1996, respectively, as compared to only 356 and 470 g/hill for the diploid PHU-STN clones. Among the diploid clones, 97% and 98% yielded significantly less than Atlantic in 1995 and 1996, respectively, and none was significantly higher.

The average specific gravity of Atlantic was 1.089 and 1.082 in 1995 and 1996, respectively, as compared to an average of 1.091 and 1.095 in the diploid clones. In the second selection cycle, 52 and 168 of the diploid clones were significantly higher in specific gravity, whereas, 37 and one were significantly lower in specific gravity than Atlantic in 1995 and 1996, respectively. Atlantic is generally considered to be a widely adapted clone. Under favorable growing conditions, however, the specific gravity of Atlantic decreased, but was accompanied by a large yield increase over unfavorable growing conditions. In regard to specific gravity, these results suggest that many of these diploid clones are widely adapted to environmental conditions. However, yields of diploid clones only increased by 32% as compared to 42% for Atlantic under favorable growing conditions, suggesting that Atlantic is more widely adapted to environmental conditions for yielding ability.

Fifty-eight clones from the second selection cycle were estimated to produce at least 5% 2n pollen. One hundred twenty-nine of the clones produced less than 1% 2n pollen, and 34 clones either failed to flower or produced too few flowers and were missed in the sampling. Jacobsen (1976) reported a logarithmic relationship between percentage of 2n pollen production in a clone and seed set per berry in 4x-2x crosses. Seed set was very poor when 2n pollen was lower than 5% in a clone, but generally satisfactory when 2n pollen was 5% or higher.

In this study, the population germplasm base between

the first and second selection cycles was kept as broad as possible by selecting from within open-pollinated seed from the clone with the highest specific gravity in each family. The second selection cycle clones from this maternal half-sib selection scheme are representative of the 72 female parents selected for high specific gravity and a random sampling of the 288 male parents selected on the basis of horticultural characteristics. Data on specific gravity were collected in two years (1990 and 1991) before selections for the highest specific gravity clone in each maternal half-sib family were made to establish the second selection cycle. It is extremely beneficial in an asexually propagated crop, such as potatoes, where individual clones can be tested in multiple years, to delay selecting for desirable characteristics until performance is evaluated for at least a couple of growing seasons prior to selecting parents for the next cycle of selection. This will result, it is hoped, in selecting parents with broad adaptability to produce the next generation.

The results of this study suggest that this diploid population can be utilized readily to contribute valuable genes for high specific gravity to the tetraploid germplasm base. Specific gravity has already been shown to be readily transmitted to tetraploid progeny through 4x-2x crosses with this germplasm (Wannamaker and Collins 1992).

Although the yield in this diploid population was significantly less than Atlantic, it remains to be seen if the lack of a negative correlation between yield and specific gravity might also be transferable to the tetraploid level. Tai (1994) has reviewed the biometrical genetic literature on unilateral sexual polyploidization and has discussed the reasons heterotic responses may or may not be observed in 4x-2x crosses.

This diploid population may be as adapted to different growing environments as Atlantic and this too, may be a trait that could be transmitted to future 4x-2x progeny. The diploids in this population were generated from a random-mating population and would be expected to have little or no inbreeding, whereas, Atlantic is inbred (Webb *et al.* 1978).

Valuable quantitative traits that are scattered across the wealth of diverse diploid germplasm available for genetic enhancement in potatoes can be exploited through basic, quantitative breeding studies conducted at the diploid level, followed by quantitative breeding studies between the tetraploid and diploid levels. Population improvement efforts at the diploid level in potatoes need to continue and be expanded.

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